The Subgenus Lentigo (Gastropoda: Strombidae) in Tropical America, Fossil and Living

PETER JUNG AND ANTOINE HEITZ

Naturhistorisches Museum, 4001 Basel, Switzerland

Abstract. The hitherto unknown occurrence of the strombid subgenus Lentigo in deposits of Neogene and Quaternary age in tropical America is documented. Sixteen species are recognized, which occur at 17 different general locations throughout the Caribbean. The oldest record is from the early middle Miocene of Carriacou, Lesser Antilles, and the youngest from the Holocene of Isla Margarita, Venezuela. Lentigo is therefore documented over a time interval of about 15 million years. Four species are described as new: S. barrigonensis from the Cubagua Formation (early Pliocene) of the Araya Peninsula, Venezuela; S. toroensis from the Cayo Agua Formation (early Pliocene) of Cayo Agua, Bocas del Toro, Panama; S. fetus from the Escudo de Veraguas Formation (late Pliocene) of Escudo de Veraguas, Bocas del Toro, Panama; and S. insulanus from the Escudo de Veraguas Formation (middle Pliocene part) of Escudo de Veraguas.

INTRODUCTION

While making up faunal lists of assemblages from the island of Escudo de Veraguas, Bocas del Toro, Panama for the Panama Paleontology Project (PPP), the senior author came across a small incomplete specimen of some kind of Strombus he thought he had never seen before. The puzzling feature of this specimen was three spiral rows of knobs on the dorsal side of the body whorl. He showed the specimen to the junior author, who almost immediately said that he remembered an article in a French journal dealing with species of Strombus showing that very feature: it was the paper by Lozouet & Maestrati (1986). In that paper the authors discussed two species of the subgenus Lentigo, Jousseaume, 1886, from the European late Eocene and Oligocene to early Miocene, respectively, stating that the late Eocene species must have given rise to the living Eastern Pacific Strombus granulatus, Swainson, 1822, since no species of Lentigo was known from the American Cenozoic. We could hardly believe this statement, and we decided to search the collections of the Basel Natural History Museum, old collections and the new PPP collections. The result was astonishing: we found a total of 43 fossil specimens of Lentigo, 26 in the old collections, and 17 in the new PPP collections. This admittedly not very rich material is here assigned to 16 "species." The word species is put in quotation marks because five of them are identified by letters only, six are positively identified, and five are identified by means of open nomenclature. Some of these "species" are represented by a single more or less well-preserved specimen or even by a fragment only. In case additional material should become available in the future, the number of species or their designation may have to be modified.

The purpose of this paper is to document the occurrences of species of the subgenus *Lentigo* in the Neogene and Quaternary of tropical America. It is not the purpose to give a revision of the subgenus.

As now understood, the subgenus *Lentigo* seems to be characterized by two features. First: *Lentigo* has three or four axial swellings per whorl on the earliest teleoconch whorls with a varying number of axial ribs in the interspaces. On succeeding whorls the axial sculptural elements become subequal in size. Second: *Lentigo* has two or more spiral rows of knobs on the dorsal side of the body whorl.

We are aware that this is not a convincing definition of the subgenus, but this goes for other subgenera of *Strombus* as well. As a matter of fact, the family Strombidae badly needs a thorough revision. We know very little about the ontogenetic development of strombid species. Careful studies of protoconchs and the sculptural development of early teleoconch whorls should be undertaken. Such studies will at the same time help the understanding of variability in strombid species. However, for the time being we are in the dark and are perhaps guessing too much.

Abbreviations

The following abbreviations are used for repository institutions and field numbers: AM, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvia, USA; BMNH, British Museum (Natural History), now The Natural History Museum London; CJ, Coates/Jackson localities; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GS, Gibson-Smith localities; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA; NMB, Na-

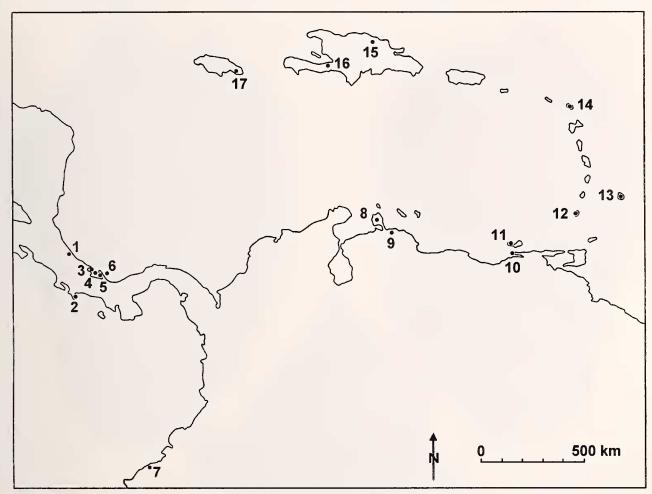


Figure 1. Fossil occurrences of the subgenus *Lentigo* in tropical America. The numbers are arranged anticlockwise (for ages see Table 1). 1. Limón, Costa Rica: S. cf. raninus. 2. Burica Peninsula, Panama: S. granulatus and S. sp. D. 3. Isla Colón, Panama: S. cf. granulatus and S. raninus. 4. Cayo Agua, Panama: S. cf. fetus Jung & Heitz, sp.nov. S. toroensis Jung & Heitz, sp.nov. 5. Valiente Peninsula, Panama: S. sp. B. 6. Escudo de Veraguas, Panama: S. fetus Jung & Heitz, sp.nov. and S. insulanus Jung & Heitz, sp.nov. 7. About 1 km west of Camarones, Esmeraldas Province, Ecuador: S. granulatus. 8. Paraguaná Peninsula, Falcón, Venezuela: S. sp. C. 9. Carrizal, Falcón, Venezuela: S. sp. A. 10. Araya Peninsula, Sucre, Venezuela: S. barrigonensis Jung & Heitz, sp.nov. 11. Isla Margarita, Nueva Esparta, Venezuela: S. raninus. 12. Carriacou, Grenadines, Lesser Antilles: S. cf. insulanus. Jung & Heitz, sp.nov. 13. Barbados: S. raninus. 14. Antigua, Lesser Antilles: S. raninus. 15. Santiago, Dominican Republic: S. aff. raninus. 16. Port-au-Prince, Haiti: S. raninus. 17. Bowden, Port Morant, Jamaica: S. sp. E.

turhistorisches Museum Basel; PJ, Peter Jung localities; PPP, Panama Paleontology Project; USNM, National Museum of Natural History, Washington, D.C., USA.

DISTRIBUTION THROUGH TIME AND SPACE

When discussing the living Indo-Pacific species of *Lentigo*, Abbott (1960:117) also assigned *Strombus aldrichi* Dall (1890:175, pl. 12, figs. 1, 4) from the early Miocene Chipola Formation of Florida to that subgenus. Lozouet & Maestrati (1986:15) disagreed with that assignment by simply stating that *S. aldrichi* is a species very different from the "radix-granulatus group."

If we presume for a moment that S. aldrichi actually

is a member of the subgenus *Lentigo*, it represents not only the oldest but also a rather isolated occurrence in the Western Hemiphere. In the original description of *S. aldrichi* Dall (1890:176) expressed the opinion that it was related to the living *S. granulatus*.

Strombus aldrichi is indeed a problem. We have eight specimens from the Chipola Formation of Florida at hand. In general shape they are similar to the material reported on herein, but their relationship to that material is not clear. As in other species of *Lentigo*, the early teleoconch whorls of *S. aldrichi* are sculptured by three axial swellings per whorl and four to eight axial ribs in the interspaces, all of which are crossed by spiral threads. On the



Figure 2. Strombus (Lentigo) lentiginosus Linnaeus. A-C. LACM 79-42.2. Intertidal - 2 m, dead coral, Korolevu, Viti Levu, Fiji (18° 13.2'S, 177°43.1'E). Height 75.3 mm, width 47.0 mm. A. Front view. B. Rear view. C. From right side. ×1.5.

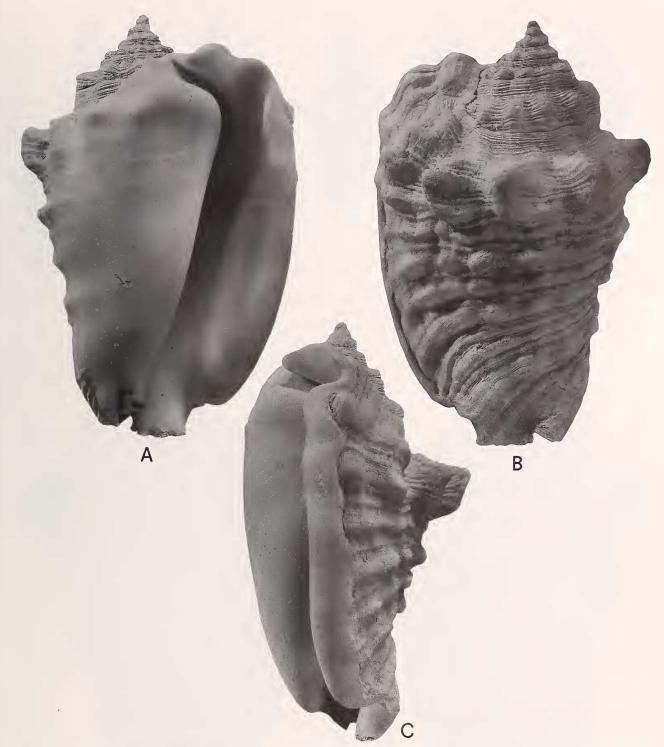


Figure 3. Strombus (Lentigo) lentiginosus Linraeus. A–C. LACM 72-138.2. Beach shells, Seychelles (5°S, 56°E). Height 75.0 mm, width 50.4 mm. A. Front view. B. Rear view. C. From right side. Comparing with Figure 2 note variability in spiral ribbing on dorsal surface of shell. ×1.5.

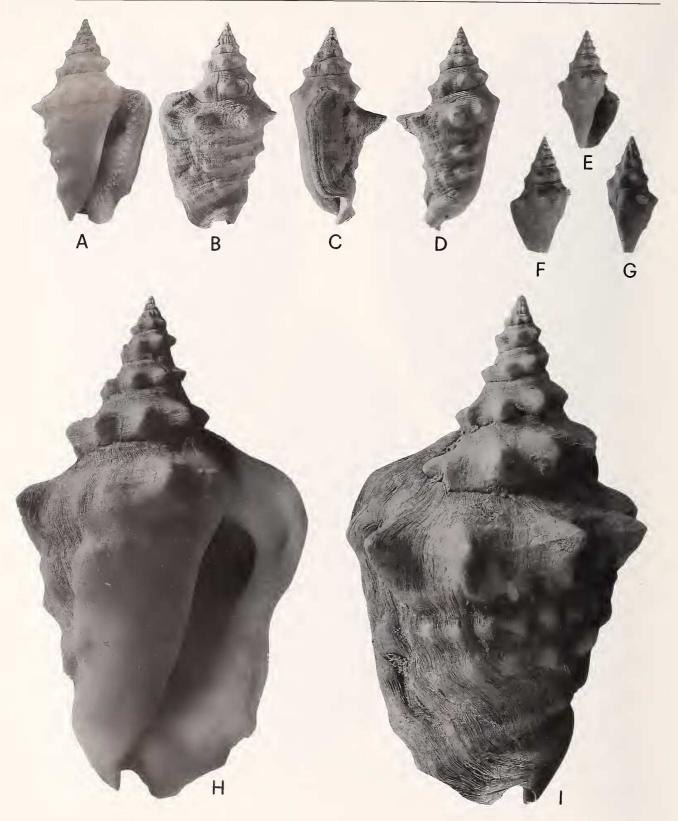


Table 1
Summary of stratigraphic occurrences of species of the subgenus *Lentigo*.

Species	Locality	Formation, Member	Age	Absolute Age in My
S. granulatus	Burica Peninsula, Panama	Armuelles Fm.	Pleistocene	0.45
	near Esmeraldas, Ecuador	upper Onzole Fm.	late Pliocene	
S. cf. granulatus	Isla Colón, Panama	unnamed	Plio-Pleistocene	1.7-3.5
S. raninus	1. Isla Colón, Panama	1. unnamed	1. Plio-Pleistocene	1.7-3.5
	Isla Margarita, Venezuela	2. Boca Chica Fm.	2. Holocene	
	3. Barbados	3. unnamed	3. Pleistocene	0.08
	4. Antigua	4. unnamed	4. Holocene	
	5. Port-au-Prince, Haiti	5. unnamed	5. Pleistocene	
S. aff. raninus	Santiago, Dominican Republic	Gurabo Fm.	early Pliocene	
S. cf. raninus	Limón, Costa Rica	Moín Fm.	Plio-Pleistocene	1.5 - 1.9
S. barrigonensis	Araya Peninsula, Venezuela	Cubagua Fm., Cerro Negro Mb.	early Pliocene	
S. toroensis	Cayo Agua, Panama	Cayo Agua Fm.	early Pliocene	4-5
S. fetus	Escudo de Veraguas	Escudo de Veraguas Fm.	late Pliocene	1.9 - 2.2
S. cf. fetus	Cayo Agua, Panama	Cayo Agua Fm.	middle Pliocene	3.5-3.6
S. insulanus	Escudo de Veraguas	Escudo de Veraguas Fm.	middle Pliocene	3.5-3.6
S. cf. insulanus	Carriacou, Grenadines	Grand Bay Fm.	early middle Miocene	
S. sp. A	Carrizal, Falcón, Venezuela	Caujarao Fm., Mataruca Mb.	late Miocene	
S. sp. B	Valiente Peninsula, Panama	Shark Hole Point Fm.	Pliocene	
S. sp. C	Paraguaná, Falcón, Venezuela	El Porvenir beds	middle/late Miocene	
S. sp. D	Burica Peninsula, Panama	Armuelles Fm.	Pleistocene	0.45
S. sp. E	Bowden, Jamaica	Bowden Fm.	early Pliocene	

other hand, *S. aldrichi* lacks the other characteristic feature of *Lentigo*: the spiral rows of knobs on the dorsal side of the body whorl. If *S. aldrichi* belongs to *Lentigo*, its distant ancestor must be one of the European species discussed by Lozouet & Maestrati (1986). One of the unknown ancestors of *S. aldrichi* must have lost (or never had) the characteristic feature of spiral rows of knobs on the dorsal side of the body whorl, which has not been reacquired since.

The 16 species recognized in this paper occur at 17 different general locations (Figure 1). The westernmost location is situated west of Limón, Costa Rica. The northernmost location is Santiago, Dominican Republic; the easternmost locality is Barbados, Lesser Antilles; and the southernmost occurrence is the Esmeraldas Province, Ecuador. In other words, the subgenus *Lentigo* is spread over a large area mostly covered by water with a northsouth extension of about 2000 km and an east-west extension of about 2500 km. The part of the Pacific Ocean

shown in Figure 1 is inhabited by *S. granulatus* and that of the Caribbean Sea by *S. raninus*.

The stratigraphic occurrences of the 16 species are listed in Table 1. The oldest record is *Strombus (Lentigo)* cf. *insulanus* n. sp. from the early middle Miocene Grand Bay Formation of Carriacou, and the youngest record is the single specimen of *S. raninus* from the Holocene Boca Chica Formation of Isla Margarita, Venezuela. The material described in this paper therefore covers a time interval of about 15 my.

SYSTEMATIC DESCRIPTIONS

Genus Strombus Linnaeus

Linnaeus, 1758:742.

Type species: (by subsequent designation, Montfort, 1810: 515):—Strombus pugilis Linnaeus, 1758:744. Recent, West Indies and Florida.

Figure 4. *Strombus (Lentigo) granulatus* Swainson. A–D. LACM 39-62.6. 4–9 m, mud and sand, Isla Taboga, Panama (8° 48′N, 79°30′W). Height 37.2 mm, width 22.4 mm. A. Front view. B. Rear view. C. From right side. D. From left side. E–G. LACM 33-121.4. Shallow water, Bahía Honda, Veraguas Prov., Panama (7°43.77′N, 81° 31.90′W). Height 21.2 mm, width 11.6 mm. E. Front view; F. Rear view G. From right side. Note that only one spiral row of knobs below the periphery is developed in this immature specimen. H–I: LACM 66-28.5. Low intertidal - 1.8 m, Bahía Partida, between Isla Partida and Isla Espiritu Santo, Gulf of California, Baja California Sur, Mexico (24° 31′N, 110° 23′W). Height 92.6 mm, width 56.7 mm. H. Front view. I. Rear view. All ×1.5.

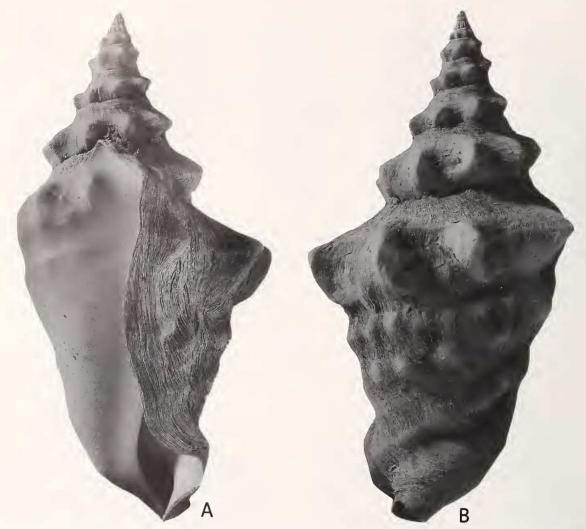


Figure 5. Strombus (Lentigo) granulatus Swainson. LACM 66-28.5. A-B. Same specimen as Figure 4H and 4I. A. From right side. B. From left side. ×1.5.

Subgenus Lentigo Jousseaume

Jousseaume, 1886:220.

Type species: (by monotypy) *Lentigo lentiginosus* Linnaeus, 1758:743. Recent. East Africa to the Marshall and Tuamotu Islands according to Abbott (1960:117).

Remarks: It is not the purpose of this paper to review the subgenus *Lentigo*, but to document its occurrence in tropical America. A proper review of *Lentigo* would require the study of much more material and from a broader geographic area. For this reason, we refrain from the attempt to give a proper diagnosis of the subgenus. However, there seem to be two features that largely define *Lentigo*. First: *Lentigo* has three or four axial swellings per whorl on the earliest teleoconch whorls with a varying number of axial ribs in the interspaces. Second: *Lentigo* has two or more spiral rows of knobs on the dorsal

side of the body whorl. Future work on the group may reveal additional diagnostic characters.

Among the species recorded herein the first feature is seen in *S. granulatus*, *S. raninus*, and *S. insulanus*. In *S. barrigonensis* and *S. fetus* it is not documented because the earliest teleoconch whorls are not preserved. Their assignment to *Lentigo* is therefore mainly based on the second feature.

Species like *Strombus pugilis* Linnaeus, 1758, and *S. alatus* Gmelin, 1791, which are assigned to the subgenus *Strombus*, or *S. gigas* Linnaeus, 1758, and *S. costatus* Gmelin, 1791, which are members of the subgenus *Tricornis* Jousseaume, 1886, all have no axial swellings on the earliest teleoconch whorls, but axial ribs of about the same size.

The stratigraphic range of *Lentigo* is late Eocene to Recent.

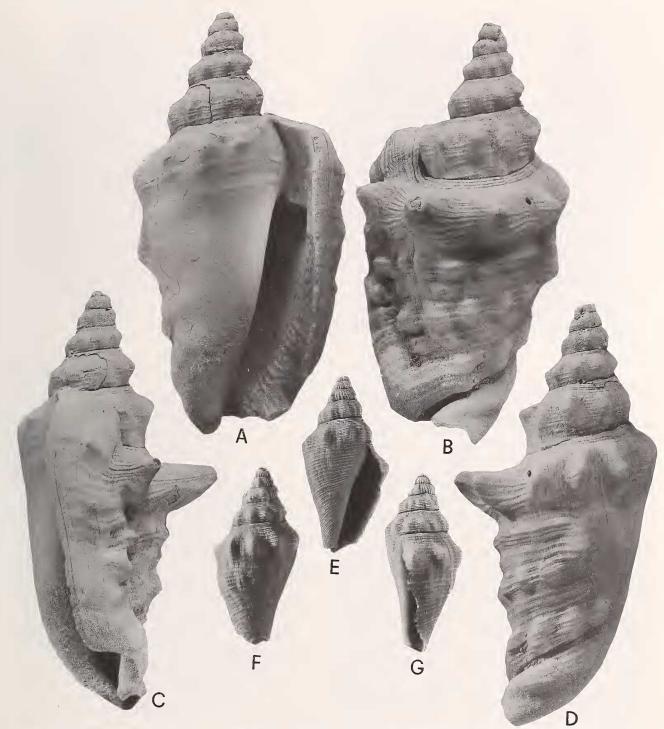


Figure 6. Strombus (Lentigo) granulatus Swainson. A–D. NMB H 17844. NMB locality 18419 (= CJ-87-04-37 = PPP 00144): east coast of Burica Peninsula, Panama; 100 m S of Boca Quebrada Corotú. Armuelles Formation (Pleistocene). Height 75.2 mm, width 40.1 mm. A. Front view. B. Rear view. C. From right side. D. From left side. E–G. NMB H 17843. NMB locality 17439: east coast of Burica Peninsula, Panama; 400 m S of Boca Quebrada Corotú. Armuelles Formation (Pleistocene). Height 31.9 mm, width 16.6 mm. E. Front view. F. Rear view. G. From right side. Note that the spiral row of knobs below the periphery is only weakly developed (compare with Figure 4E–G). Both specimens ×1.5.

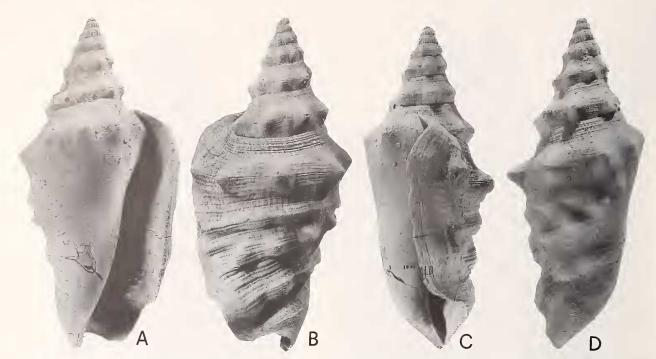


Figure 7. Strombus (Lentigo) granulatus Swainson. A-D. BMNH PI TG 4731: road-cutting about 1 km west of village of Camarones, Esmeraldas Province, Ecuador. Upper Onzole Formation (late Pliocene) (for general location see number 7 of Figure 1). Height 58.4 mm, width 29.0 mm. A. Front view. B. Rear view. C. From right side. D. From left side. ×1.5.

Strombus (Lentigo) lentiginosus Linnaeus

(Figures 2, 3)

Strombus lentiginosus Linnaeus, 1758:743.
Strombus (Lentigo) lentiginosus Linnaeus, Abbott, 1960:
117, pl. 17, figs. 11, 12; pl. 94, fig. 4. For additional citations see this publication. Lozouet & Maestrati, 1986:12, fig. (unnumbered).

Remarks: We have received two specimens of this species on loan from the Los Angeles County Museum of Natural History. One specimen is from the Seychelles (LACM 72-138.2), the other from Korolevu, Viti Levu, Fiji (LACM 79-42.2). Both are illustrated here for comparison with a fossil specimen from the island of Escudo de Veraguas, Bocas del Toro, Panama (see under Strombus (Lentigo) fetus n. sp.).

Depth range and substratum: From low tide mark to about 12 feet, usually on a coral sand bottom which may be rocky and with weeds (Abbott, 1960:117).

Geographic distribution: From East Africa to the Marshall and Tuamotu Islands (Abbott, 1960:117, pl. 96).

Strombus (Lentigo) granulatus Swainson (Figures 4–10)

Strombus granulatus Swainson, 1822:43, and Appendix, p. 8. Strombus (Lentigo) granulatus Swainson, 1822, Emerson &

Old, 1963:7, figs. 4, 6–8 (for additional citations see this publication), Keen, 1971:421, fig. 608. Abbott, 1974:144, color plate 4, fig. 1582. Lozouet & Maestrati, 1986:11, 12, figs. A–D.

Strombus granulatus Mawe, 1823:125, 127, pl. 25, fig. 3. Grant & Gale, 1931:755 (for additional citations see this publication). Durham, 1950:117, pl. 27, figs. 3, 8. Strombus granulatus acutus Durham, 1950:118, pl. 27, figs.

1, 2, 5 (not Perry, 1811, pl. 12, fig. 2).

Strombus granulatus cortezianus Durham, 1962:213.

Description: Shell reaching a height of about 90 mm,

moderately slender. Protoconch with five rapidly enlarging smooth volutions. Profile of first three volutions flat, of fourth and fifth volution, convex. On second third volution of protoconch there is an indication of a spiral ornamentation near abapical suture. Dividing line between protoconch and teleoconch slightly opisthocyrt. Number of teleoconch whorls up to about eight. Initial sculpture of teleoconch consists of 11 to 13 spiral threads overriding less closely spaced axial riblets. Spiral threads sometimes-but not always-seen to extend backward a little distance beyond outer lip of protoconch. First two and a half to three and a half teleoconch whorls sculptured by three to four varices per whorl. Interspaces of varices with three to five axial ribs. Varices and axial ribs over-ridden by spiral threads. Varices gradually lost and replaced by axially elongated projections numbering nine

or 10 per whorl. On last teleoconch whorls these projec-

tions are developed as pointed spines. Dorsal surface of

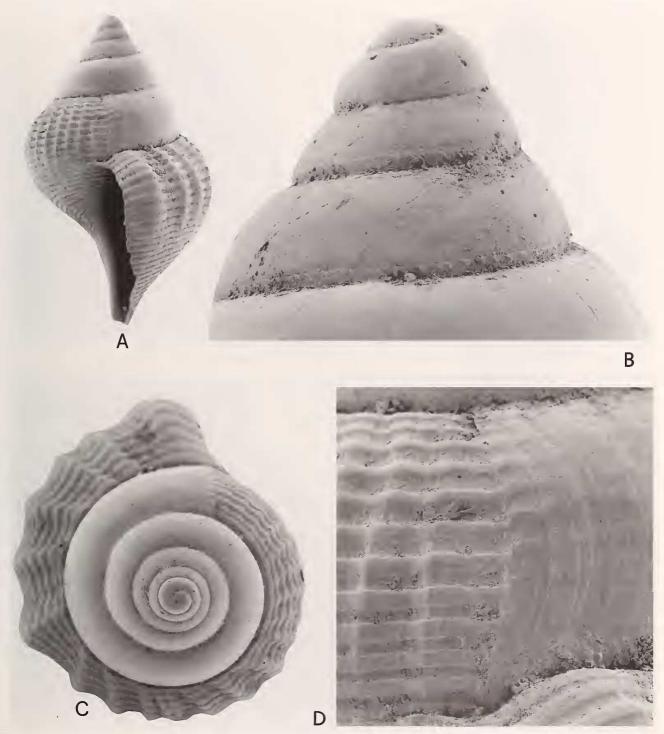


Figure 8. Strombus (Lentigo) granulatus Swainson. A–D. LACM 72-59.4. 75 feet, gravel and cobble, small islets off Quepos, Puntarenas Province, Costa Rica (9°22′12″N, 84°09′15″W). A. From right side showing protoconch and first teleoconch whorl, ×35. B. Enlargement of protoconch, ×200. Note spiral sculpture near abapical suture. C. Apical view, ×55. Note spiral ribs of teleoconch under outer lip of protoconch. D. Transition from protoconch to teleoconch, ×160. Note opisthocyrt growth lines of protoconch.

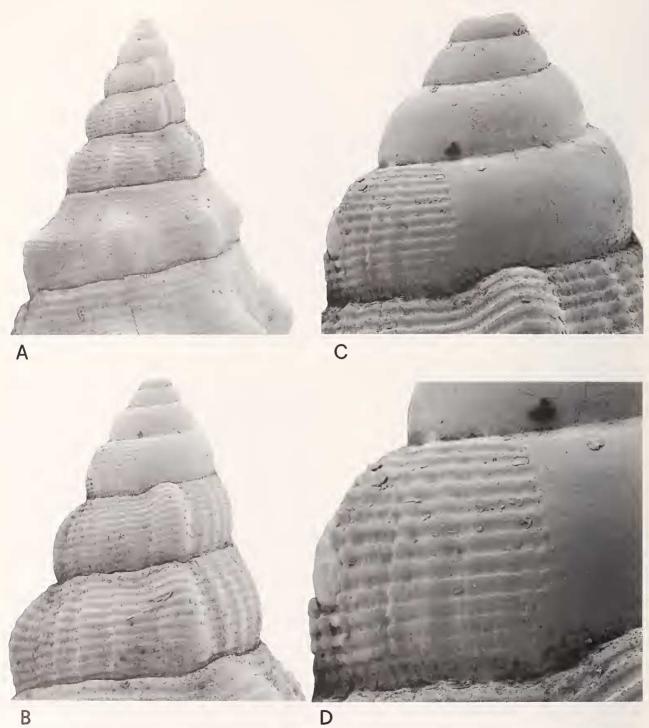


Figure 9. Strombus (Lentigo) granulatus Swainson. A–D. NMB H 17853. Dredged in 40 to 45 feet, Isla Pedro González, Archipiélago de las Perlas, Panama. A. Incomplete protoconch and early teleoconch whorls, ×12. Note development of varices into subequal axial ribs and finally into axially elongated, slightly pointed knobs. B. Enlargement of same view as A, ×30. C. Enlargement of incomplete protoconch, ×70. D. Transition from protoconch to teleoconch, ×130. In this specimen no spiral ribs of the teleoconch are visible under the outer lip of the protoconch.

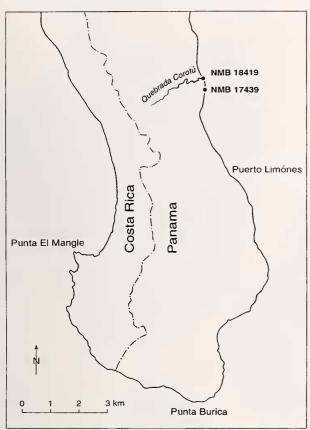


Figure 10. Map of the southern part of the Burica Peninsula, Chiriquí Province, Panama (for general location see number 2 of Figure 1). *S. granulatus* occurs at NMB localities 17439 and 18419, whereas *S.* sp. D has been found only at NMB locality 17439.

body whorl sculptured by three spiral rows of knobs sometimes over-ridden by spiral threads. Interspaces of rows of knobs sometimes—but not always—with three spiral threads. Aperture long and narrow. Parietal callus smooth. Outer lip somewhat flaring, its inner surface with a band of granulations. Lower part of outer lip with a moderately deep sinus. Base of columella bent backward.

Type: Not known. According to a letter from Kathie Way dated September 16, 1996, the type of this species is not in the collections of the Department of Zoology of The Natural History Museum, London; it was suggested that we inquire at the Department of Zoology of the National Museum of Wales in Cardiff, but Alison Trew of that institution gave a negative answer (letter dated September 26, 1996).

Remarks: We have studied a small number of Recent specimens of this species. We were especially interested in immature specimens in order to get photographs of complete protoconchs (Figure 8A–D) and to be able to



Figure 11. Strombus (Lentigo) cf. granulatus Swainson. NMB H 17847. NMB locality 18544 (= CJ-93-21-01 = PPP 01259); Ground Creek, northwestern part of Isla Colón, Bocas del Toro, Panama. Plio-Pleistocene. Height 80.8 mm. Fragment viewed from left side, ×1.5.

recognize the development of the sculpture on early teleoconch whorls. As hinted at in the above description, it is interesting to observe that the earliest spiral sculpture is sometimes developed already under the outer lip of the protoconch. The surface of the protoconch is smooth with the exception of some opisthocyrt growth lines near the outer lip and an ill-defined spiral sculptural element close to the abapical suture of the second and third volution.

The size of the adult shell and the intensity of the spiral sculpture are quite variable. Large specimens (height around 90 mm) have about eight teleoconch whorls, whereas small adult shells (height around 35 mm) have seven or seven and a half teleoconch whorls. These smaller adult shells are sometimes designated "dwarf variety" on museum labels. It would take a detailed statistical study based on a large amount of material to prove or disprove the existence of intermediates. For the time being *S. granulatus* is considered a variable species em-

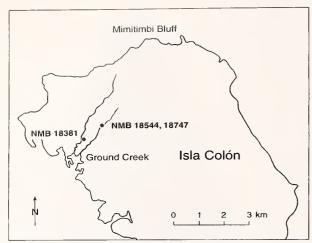


Figure 12. Map of the northern part of Isla Colón, Bocas del Toro, Panama, showing NMB localities 18381 and 18544, where *S. cf. granulatus* has been found, and NMB locality 18747, where *S. raninus* is recorded from (for general location see number 3 of Figure 1).

bracing large and small forms, a view also adopted by Emerson & Old (1963:9). Only four fossil specimens of this species are available: two from the Armuelles Formation (Pleistocene) of the southern Burica Peninsula, Panama, and two from the upper Onzole Formation (late Pliocene) of west of Camarones, Esmeraldas Province, Ecuador (Whittaker, 1988, fig. 2).

Comparisons: *Strombus granulatus* is the only species of the subgenus *Lentigo* in the Eastern Pacific. Occasional comparative remarks will be found under the fossil species discussed herein.

Material: For this paper we have used 16 lots with a total of 30 specimens as listed below:

- 6 spec., LACM 33–121.4: shallow water, Bahía Honda, Veraguas, Panama (7° 43.77′N, 81° 31.90′W).
- 2. 3 spec., LACM 39-62.6: 4-9 m, mud and sand, Isla Taboga, Panama (8° 48'N, 79°30'W).
- 1 spec., LACM 66–28.5: low intertidal 1.8 m, Bahía Partida, between 1sla Partida and Isla Espiritu Santo, Gulf of California, Baja California Sur, Mexico (24° 31'N, 110°23'W).
- 4. 7 spec., LACM 72–59.4: 75 feet, gravel and cobble, small islets off Quepos, Puntarenas, Costa Rica (9°22′ 12″N, 84° 9′ 15″W).
- 1 spec., Alvarez coll. 09873: Islas Secas, Golfo de Chiriquí, Panama. Dredged in 30 m.
- 1 spec., Alvarez coll. 07564: Isla de los Pajaros, Archipiélago de las Perlas, Panama. Dredged in 45 feet.
- 1 spec., Alvarez coll. 06572: Isla Saboga, Archipiélago de las Perlas, Panama. Dredged in 40–50 feet.
- 1 spec., Alvarez coll. 06732: Isla Saboga, Archipiélago de las Perlas, Panama. Dredged in 28–35 feet.

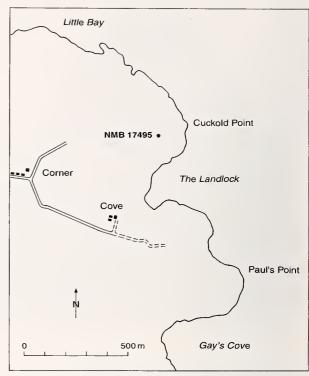


Figure 13. Map of part of northeastern Barbados, Lesser Antilles, showing NMB locality 17495, where *S. raninus* has been found (for general location see number 13 of Figure 1).

- 1 spec., Alvarez coll. 09872: Islas Secas, Golfo de Chiriquí, Panama. Dredged in 30 m.
- 10. 1 spec., Alvarez coll. 09775: Isla Coiba, Golfo de Chiriquí, Panama. Dredged in 30–32 m.
- 11. 1 spec., Alvarez coll. 09675 (NMB H 17866): Isla Montuosa, Golfo de Chiriquí, Panama. Dredged in 25–30 m.
- 12. 1 spec., Alvarez coll. 02175 (NMB H 17867): Bahía San Telmo, Archipiélago de las Perlas, Panama. Dredged in 20–25 feet.
- 13. 1 spec., Alvarez coll. 2286 (NMB H 17853): Isla Pedro González, Archipiélago de las Perlas, Panama. Dredged in 40–45 feet.
- 14. 1 spec., NMB H 17843, NMB locality 17439 (= PJ 1757): 400 m S of Boca Quebrada Corotú, Burica Peninsula, Panama. Armuelles Formation (Pleistocene).
- 15. 1 spec., NMB H 17844, NMB locality 18419 (= CJ-87-04-37 = PPP 00144): 100 m S of Boca Quebrada Corotú, Burica Peninsula, Panama. Armuelles Formation (Pleistocene).
- 16. 2 spec., BMNH PI TG 4731-2: road-cutting about 1 km west of the village of Camarones, Esmeraldas Province, Ecuador. Upper Onzole Formation (late Pliocene).

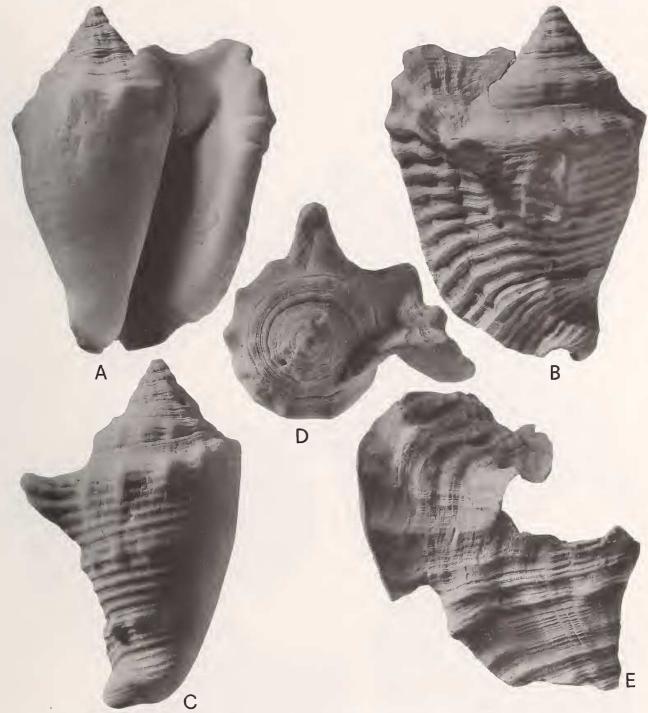
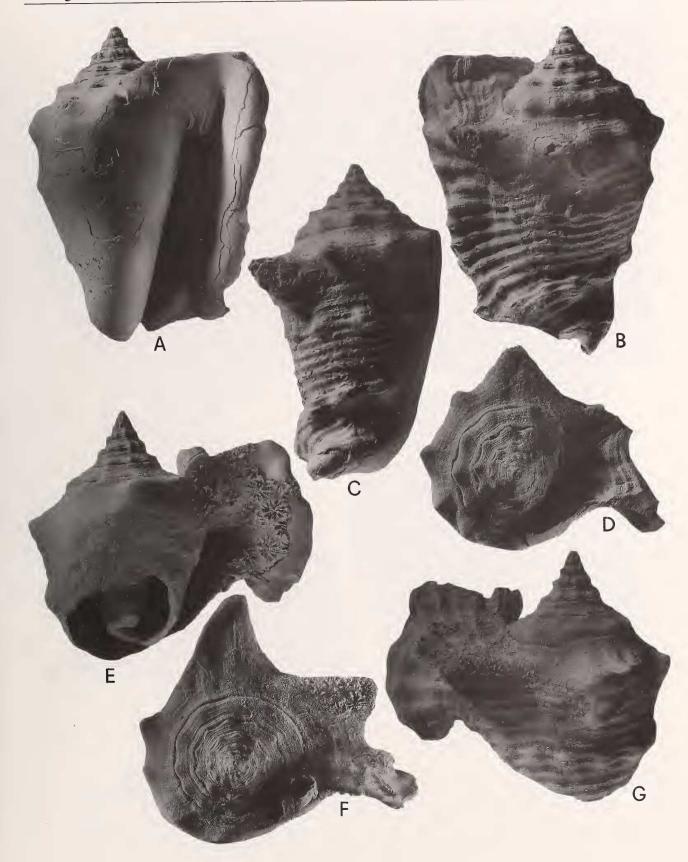


Figure 14. Strombus (Lentigo) raninus Gmelin. A–D. NMB H 17859. NMB locality 18750: Plantain Cays, outer coast of Valiente Peninsula, Bocas del Toro, Panama. Recent. Height 63.7 mm, width 46.9 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. E. NMB H 17857. NMB locality 18747: Ground Creek, Isla Colón, Bocas del Toro, Panama. Pleistocene. Height 60.6 mm, width 48.5 mm. Rear view. Both specimens ×1.5.



Figure 15. Strombus (Lentigo) raninus Gmelin. A-D. NMB H 17860. NMB locality 17692: Islas Chimanas, Estado Anzoategui, Venezuela. Recent. Height 64.1 mm, width 44.8 mm, A. Front view. B. Rear view. C. From left side. D. Apical view. ×1.5.

Figure 16. Strombus (Lentigo) raninus Gmelin. A–D. NMB H 17861. NMB locality 17564: Laguna Boca Chica, Isla Margarita, Venezuela. Type locality of Boca Chica Formation (Holocene terrace). Height 58.9 mm, width 45.5 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. E–G: NMB H 17856. NMB locality 18747: Ground Creek, Isla Colón, Bocas del Toro, Panama. Pleistocene. Height 45.8 mm, width 51.1 mm. E. Front view. F. Apical view. G. Rear view. Both specimens ×1.5.



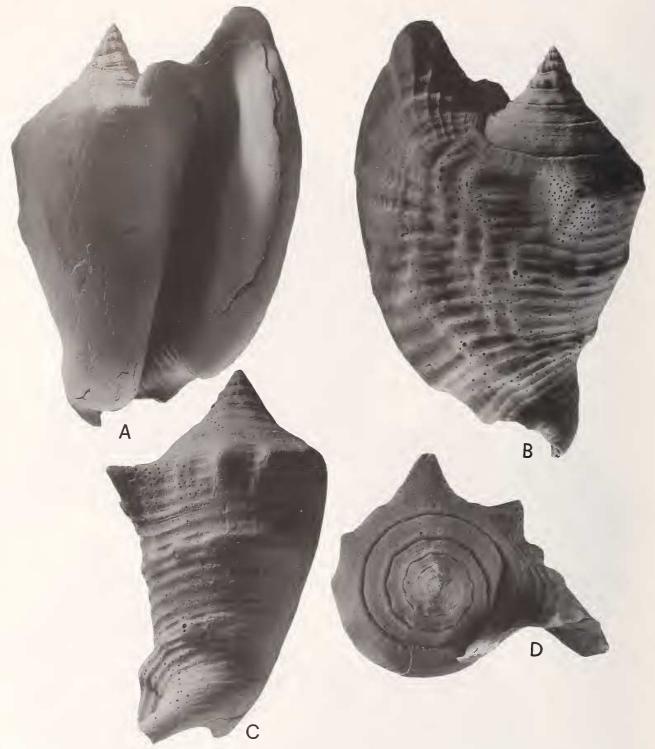


Figure 17. Strombus (Lentigo) raninus Gmelin. A–D. NMB H 17862. NMB locality 18940: Champ de Tir (rifle-range), Port-au-Prince, Haiti. Pleistocene. Height 80.0 mm, width 51.7 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. ×1.5.

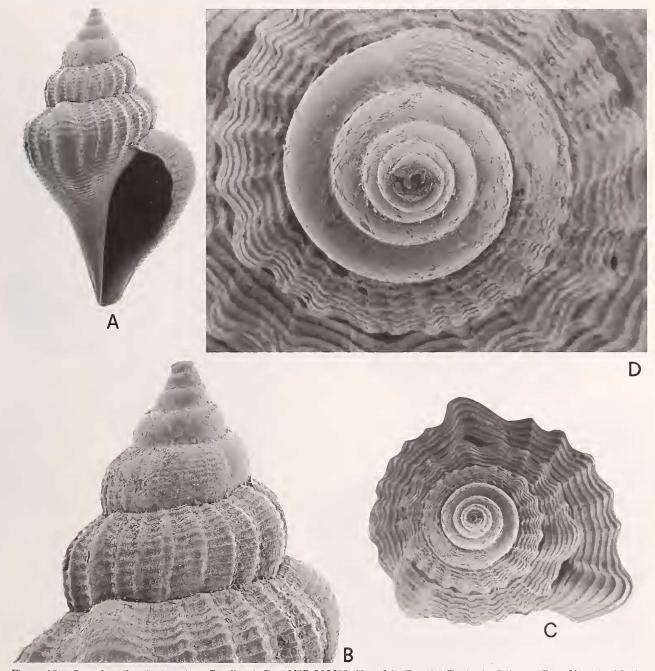


Figure 18. Strombus (Lentigo) raninus Gmelin. A–D. ANSP 285500. Near Isla Cancún, Territorio Quintana Roo, Yucatán, Mexico. Recent. A. Front view showing protoconch and the first three teleoconch whorls. ×12. B. Enlargement of same view showing transition from protoconch to teleoconch and sculpture of early teleoconch whorls. ×30. C. Apical view showing three varices per whorl. ×20. D. Enlarged apical view. The initial volution of the protoconch is damaged. The protoconch seems to consist of four and a half to five volutions. ×60.

Depth range and substratum: On exposed beaches of rock and sand; common in shallow water down to 75 m (Keen, 1971:421; Abbott, 1974:144).

Geographic distribution: The northern end of the Gulf

of California to Ecuador (Keen, 1971:421) and Galápagos Islands (Grant & Gale, 1931:755).

Occurrence: The Pliocene and Pleistocene occurrences of this species in Baja California, Mexico, have been list-



ed by Emerson & Old (1963:11). In Panama it is documented from two adjacent localities in the Armuelles Formation (Pleistocene) situated on the east coast of the Burica Peninsula (Figure 10). In Ecuador it is reported from the upper Onzole Formation (late Pliocene) of west of Camarones, Esmeraldas Province.

Strombus (Lentigo) cf. granulatus Swainson (Figures 11, 12)

Remarks: Two fragmentary specimens are available. Both consist of the lower and strongly bent backward part of the columella, a portion of the parietal wall, and a small part of the dorsal surface of the body whorl.

The larger specimen has been photographed from the left side in order to show the lowest spiral row of knobs. The knobs are over-ridden by spiral threads. The specimen is of considerable size. Comparing it with a large Recent shell of *S. granulatus* it is estimated that it must have reached a height of about 120 mm.

The second specimen is smaller, but the preserved part of the dorsal surface of the body whorl is somewhat larger than that of the other specimen. It shows the beginning of a second spiral row of knobs.

Occurrence: NMB localities 18544 (= CJ-93-21-01 = PPP 01259) and 18381 (= PJ 2150 = CJ-93-56-01 = PPP 01286): both Ground Creek, nortwestern part of Isla Colón, Bocas del Toro, Panama (Figure 12). Beds of Plio-Pleistocene age.

Strombus (Lentigo) raninus Gmelin (Figures 12–18)

Strombus raninus Gmelin, 1791:3511; Bales, 1942:18, pl. 4, fig. c; Rice & Kornicker, 1962: 373, pl. 5, figs. 5, 10; Shoemaker, 1971:72; Humfrey, 1975:101, pl. 8, figs. 5, 5a–c; Odé, 1982:16.

Strombus tuberculatus Lamarck, 1822:690.

Strombus (Strombus) raninus Gmelin, Clench & Abbott, 1941:2, pl. 2.

Strombus (Tricornis) raninus Gmelin, Abbott, 1974:144, no. 1585, color plate 4.

Strombus raninus nanus Bales, 1942:19, pl. 4, figs. a-b. Strombus wilsonorum Petuch, 1994:75, pl. 16, fig. K and p. 84, explanation of pl. 21, and p. 263.

Description: Shell solid, reaching a height of around 100 mm. Protoconch consists of about four and a half to five smooth volutions. Number of teleoconch whorls nine and a half. The first two to three teleoconch whorls usually

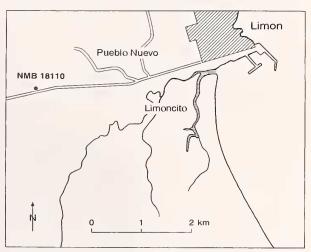


Figure 20. Map of the area of Limón, Costa Rica, showing NMB locality 18110, where *S.* cf. *raninus* has been found (for general location see number 1 of Figure 1).

with three primary axial ribs per whorl but sometimes without varices, i.e., with subequal axial ribs only. Space between primary axial ribs with three to seven secondary axial riblets. All the axial ribs and riblets are crossed by up to 10 spiral threads. On successive whorls the axial ribs gradually become subequal in size and are reduced to knobs situated on the shoulder of the whorl. The number of spiral threads on the spire whorl is somewhat reduced and their width is not equal. The two last knobs on the shoulder of the body whorl are spinelike and thus much larger than all the other knobs. Dorsal surface of body whorl sculptured by numerous fairly prominent spiral threads and two spiral rows of knobs. The abapical row ends near the edge of the outer lip at the position of the moderately deep stromboid notch. The adapical row of knobs is situated a little above the middle of the space between the abapical row and the shoulder of the body whorl. Outer lip thickened, its adapical end extended to below the position of the apex, in rare cases above it. Outer lip smooth except for some lirae at end below the stromboid notch and two to three ridges at the adapical end of the aperture. Parietal wall smooth. Base of columella strongly bent backward.

Type: Not known. Clench & Abbott (1941:3) selected a "type figure."

Type locality: Clench & Abbott (1941:3) designated

Figure 19. Strombus (Lentigo) aff. raninus Gmelin. A-D. NMB H 17806. NMB locality 18952 (= TU 1206): roadcut at K 17, highway from Santiago to San José de las Matas, west of bridge over Río Yaque del Norte at Santiago de los Caballeros, Dominican Republic. Gurabo Formation (probably early Pliocene part). Height 77.3 mm, width 67.4 mm. A. Front view. B. Rear view. C. From right side. D. Apical view. ×1.5.

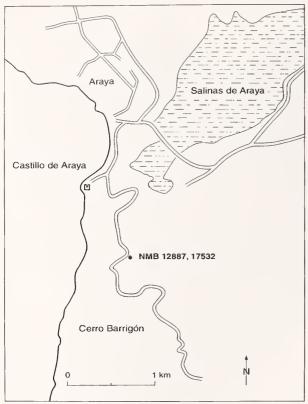


Figure 21. Map of area north of Cerro Barrigón, westernmost Araya Peninsula, Venezuela, showing NMB localities 12887 and 17532, where *S. barrigonensis* Jung & Heitz, sp. nov. has been found (for general location see number 9 of Figure 1).

Puerto Plata on the north coast of the Dominican Republic as the type locality.

Remarks: As indicated in the description, the axial sculpture of the early teleoconch whorls is strongly variable. There may be varices or not. When varices are present, their number is not constant. The limited amount of material studied for this paper does not allow us to be more precise except that we have seen rare specimens with four varices on early teleoconch whorls. The fact that there are specimens without varices at all might imply that the variability of the number of varices reaches from zero to four. However we have not seen specimens with one or two varices per early teleoconch whorl.

The above description is based on recent specimens from the Gibson-Smith collection and fossil specimens from six different locations (see under "Material"). Unfortunately, no well preserved protoconchs are available. Recent shells show some variability. Thus the extension of the adapical end of the outer lip is variable and there may be only one spinelike knob on the shoulder of the body whorl. *S. wilsonorum* Petuch (1994:75, pl. 16, fig. K and p. 84, explanation of pl. 21, and p. 263) from the Pleistocene of Florida clearly is a synonym of *S. raninus*.

The figured holotype closely resembles the specimen cited below from the Pleistocene of Haiti (Figure 16A–D).

Petuch (1994:75, pl. 16, fig. E and p. 84, explanation of pl. 21) assigned *S. raninus* to the subgenus *Lobatus* Iredale (1921:208). The name *Lobatus*, however, is an historical accident as explained by Abbott (1960:53) and is not available for a strombid subgenus.

As far as we are aware *S. raninus* has never been reported as a fossil (except for *S. wilsonorum* cited above). For this reason we are going to comment briefly on these fossil specimens from six different localities.

First: Two fragmentary specimens are available from the Pleistocene of Isla Colón, Bocas del Toro, Panama (NMB locality 18747: Figure 12). One has the adapical part of the outer lip and a portion of the dorsal side of the body whorl preserved (Figure 14E). The other consists of the spire and the adapical part of the body whorl (Figure 16E–G). The protoconch and the earliest teleoconch whorls of the latter are missing, and the first preserved teleoconch whorls are strongly eroded. One spiral row of knobs on the dorsal side of the body whorl can be recognized. A third specimen from the Pleistocene of Isla Colón (NMB locality 18381) is identified as *S. raninus* Gmelin? It is a well preserved fragment representing parts of the spire, but it is too incomplete for positive identification.

Second: There is single specimen from the Pleistocene of the neighborhood of Port-au-Prince, Haiti (NMB locality 18940) (Figure 17A–D). The protoconch and the first one or two teleoconch whorls are missing, but otherwise it is practically complete. Its surface is somewhat worn. The extension of the adapical end of the outer lip reaches above the apex, and the last knob on the shoulder of the body whorl is smaller than the second-last.

Third: An almost complete specimen (Figure 16A–D) has been collected from the Holocene of Isla Margarita, Venezuela (NMB locality 17564). The protoconch and the first teleoconch whorls are missing, and the edge of the outer lip, as well as the last knob on the shoulder of the body whorl, is somewhat damaged.

Fourth: A single specimen (NMB H 17873) with a broken apex and partly broken dorsal surface has been collected from a late Pleistocene terrace on the northeast coast of Barbados (NMB locality 17495: Figure 13). In an unpublished study by P. Büsser (University of Berne, 1980) an age of 82,000 years was assigned to this terrace. Two fairly well-preserved specimens from the Pleistocene of Bishopscourt, Barbados, are contained in the collections of the BMNH (G 10888).

Fifth: In the collections of the BMNH (GG 4921) there is an incompletely preserved specimen collected from a yellow marl of Holocene age of an unspecified locality on the island of Antigua.

Sixth: In February 1998, Dr. Jon Todd of the BMNH collected six fragments from the late Pliocene part of the Moín Formation of the Limón area, Costa Rica. One of



Figure 22. Strombus (Lentigo) barrigonensis Jung & Heitz, sp. nov. A–D. NMB locality 12887: north slope of Cerro Barrigón, Araya Peninsula, Venezuela. Cerro Negro Member of Cubagua Formation (early Pliocene). A. NMB H 17849. Paratype. Height 70.5 mm. Rear view. B–D NMB H 17848. Holotype. Height 81.6 mm, width 51.4 mm. B. Front view. C. Rear view. D. From left side. Both specimens ×1.5.

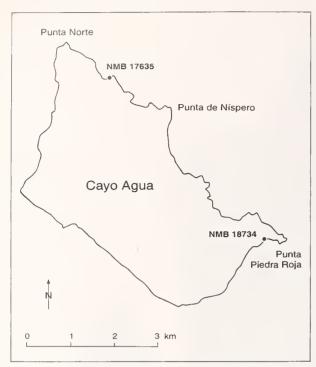


Figure 23. Map of Cayo Agua, Bocas del Toro, Panama, showing NMB locality 17635, where *S. toroensis* Jung & Heitz, sp. nov. has been found, and NMB locality 18734, from where *S.* cf. *fetus* Jung & Heitz, sp.nov. is recorded (for general location see number 4 of Figure 1).

the specimens is complete enough to be positive about the identification. Another fragment shows the spire with parts of the protoconch preserved.

Comparisons: *S. raninus* is morphologically dissimilar to any of the species discussed herein. *S. fetus* n. sp. has somewhat similar proportions but lacks the spinelike knobs on the shoulder of the body whorl.

Clench & Abbott (1941:3) considered *S. raninus* and *S. gallus* Linnaeus (1758:743) as closely related species. This statement was probably based on the long extension of the adapical end of the outer lip. This extension may be extreme in *S. gallus* but never is in *S. raninus*. More importantly, *S. gallus* never has spiral rows of knobs on the dorsal side of the body whorl. We consider the latter feature as diagnostic for the subgenus *Lentigo*. *S. gallus* is therefore not included in *Lentigo*.

Material: For this paper we have used 20 lots with a total of 58 specimens as listed below:

- 1. 15 spec., NMB locality 17663: Punta La Salina (El Pico), west coast of the Paraguaná Peninsula, Falcón, Venezeula. Recent.
- 11 spec., NMB locality 17675: between Naval Base of Puerto Cabello and Playa Quizandal, Borburata, Estado Carabobo, Venezuela. Recent.
- 3. 2 spec., NMB locality 17679: beach immediately

- west of Playa Grande Yacht Club, Distrito Federal, Venezuela. Recent.
- 2 spec., NMB locality 17685: about 1 km NE of Carenero, Laguna de Buche, Estado Miranda, Venezuela. Recent.
- 3 spec., NMB locality 17686: Bahía Los Totumos, between Carenero and Cabo Codera, Estado Miranda, Venezuela. Recent.
- 6. 3 spec., NMB H 17860, NMB locality 17692: Islas Chimanas, Estado Anzoategui, Venezuela. Recent.
- 2 spec., NMB locality 17700: Islas Los Roques, Venezuela. Recent.
- 8. 1 spec., NMB locality 17702: Isla La Tortuga, Venezuela. Recent.
- 1 spec., NMB H 17859, NMB locality 18750: Plantain Cays, outer coast of the Valiente Peninsula, Bocas del Toro, Panama. Recent.
- 2 spec., ANSP 285500: near Isla Cancún, Territorio Quintana Roo, Yucatán, Mexico. Recent.
- 3 spec., FMNH 177106: Lake Worth, Palm Beach County, Florida, USA. Recent.
- 12. 1 spec., USNM 269542: off Miami, Florida, USA. Recent.
- 13. 3 spec., USNM 890017: Peanut Island, Lake Worth, Florida, USA. Recent.
- 14. 1 spec., NMB H 17861, NMB locality 17564: Laguna de Boca Chica, Isla Margarita, Venezuela. Type locality of Boca Chica Formation (Holocene terrace). See Macsotay & Moore (1974:34, 41).
- 15. 1 spec., NMB H 17862, NMB locality 18940: Champ de Tir (= rifle-range), Port-au-Prince, Haiti. Pleistocene
- 2 spec., NMB H 17856 and H 17857, NMB locality
 18747 (= PJ 2284 = PPP 02250): Ground Creek, Isla
 Colón, Bocas del Toro, Panama. Pleistocene.
- 17. 1 spec., NMB H 17873, NMB locality 17495: Barbados, northeast coast; near "The Landlock." Coordinates: 662.250E/1471.780N. Terrace of young Pleistocene age.
- 18. 2 spec., BMNH G 10888: Bishopscourt, Barbados. Low level reefs, Pleistocene.
- 1 spec., BMNH GG 4921: unspecified locality on Antigua, Lesser Antilles. From a yellow marl of Holocene age.
- 20. 6 spec., BMNH PI TG 4733/38: Route 32, 3 km west of Puerto Limón, Costa Rica. Basal Moín Formation, late Pliocene (1.5–1.9 my).

Depth range: 1 foot (0.3 m) (Humfrey, 1975:102) to 30 fathoms (about 55 m) (Odé, 1982:16).

Substratum: On offshore coral reefs and somewhat deeper algal environment (Odé, 1982:16); on eel grass beds (Humfrey, 1975:102); on grassy bottoms (Rios, 1985:62).

Geographic distribution: North Carolina to Florida,

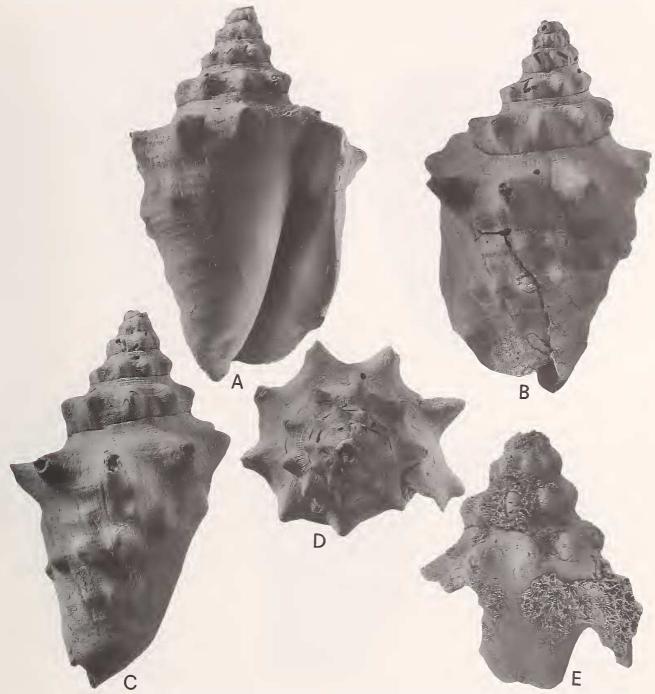


Figure 24. Strombus (Lentigo) toroensis Jung & Heitz, sp. nov. A–E. NMB locality 17635; northeast coast of Cayo Agua, Bocas del Toro, Panama; about 1.3 km southeast of Punta Norte. Cayo Agua Formation (early Pliocene). A–D. NMB H 17865. Holotype. Height 69.3 mm, width 42.3 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. E. NMB H 17845. Paratype. Height 47.2 mm, width 41.7 mm. Front view. Both specimens ×1.5.

Bermuda (Odé, 1982:16), Gulf of Mexico (Springer & Bullis, 1956:26; Lipka, 1974:150), West Indies, northern Colombia, Venezuela, Surinam, Brasil (Amapá to Rio Grande do Norte) (Rios, 1985:62).

Occurrence: The fossil occurrences include the late Pliocene of the Limón area, Costa Rica; the Pleistocene of Isla Colón, Bocas del Toro, Panama; the Pleistocene near Port-au-Prince, Haiti; the late Pleistocene of Barbados;

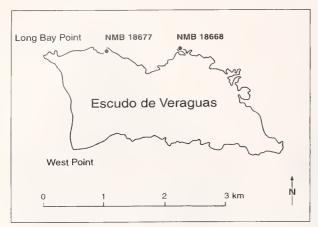


Figure 25. Map of the island of Escudo de Veraguas, Bocas del Toro, Panama, showing NMB locality 18677, where *S. fetus* Jung & Heitz, sp. nov. has been found, and NMB locality 18668, from where *S. insulanus* Jung & Heitz, sp. nov. is recorded (for general location see number 6 of Figure 1).

the Holocene (Macsotay & Moore, 1974:34, 41) of Isla Margarita, Venezuela, and the Holocene of Antigua.

Strombus (Lentigo) aff. raninus Gmelin (Figure 19)

Remarks: A single fairly complete and fairly well-preserved specimen is available. It is the only specimen of *Lentigo* known from the Dominican Republic; it had been collected by Harold and Emily Vokes from a locality (TU 1206) near Santiago. Vokes (1989:46) assigned this locality to the Gurabo Formation.

The protoconch of the specimen is incomplete. The lirae on the abapical part of the outer lip and the sharp, elevated lirae near the adapical canal of the aperture are practically the same as those of *S. raninus*. However, the early teleoconch whorls carry only three primary axial ribs and not four as in *S. raninus*. But the main difference between the two species concerns the general shape of the spire. In *S. raninus* the spire is rather high, whereas in *S.* aff. raninus it is sunken. In other words, the slope of the last three teleoconch whorls in *S. raninus* is steep, but in *S.* aff. raninus rather flat.

Occurrence: NMB locality 18952 (= TU 1206): roadcut at K 17, highway from Santiago to San José de las Matas, west of bridge over Río Yaque del Norte at Santiago de los Caballeros, Dominican Republic (see Saunders et al., 1986:64), Gurabo Formation (probably early Pliocene part).

Strombus (Lentigo) cf. raninus Gmelin (Figure 20)

Remarks: Two fragmentary specimens are available. Both are too incomplete to be figured. The larger frag-

ment (height 38.2 mm) (NMB H 17874) consists of the columella, part of the spire, and a small part of the dorsal surface of the body whorl carrying the beginning of a spiral row of knobs. The smaller fragment (height 15.4 mm, width 9.9 mm) (NMB H 17875) consists of a few spire whorls.

Occurrence: NMB locality 18110 (= PJ 2033 = CJ-89-38-2 = PPP 00718); about 2 km west of Cementerio of Limón, Costa Rica; north side of main road (Figure 20). Moín Formation (late Pliocene).

Strombus (Lentigo) barrigonensis Jung & Heitz, sp. nov.

(Figures 21, 22)

Etymology: Named after Cerro Barrigón, near the western end of the Araya Peninsula, Venezuela.

Description: Shell reaching a height of about 80 mm, moderately slender. Protoconch and earliest teleoconch whorls not known. Earliest preserved teleoconch whorls sculptured by eight axial ribs per whorl, which are overridden by eight spiral threads. On later teleoconch whorls the axial ribs gradually develop into knobs and on the dorsal side of the body whorl into spines. Number of knobs or spines on last whorl 10. Number of spiral threads on penultimate whorl 13. Number of preserved teleoconch whorls seven. Dorsal surface of body whorl with three spiral rows of knobs. The most adapically situated row not prominent, the others prominent. Remainder of dorsal side of body whorl sculptured by spiral and axial threads. Aperture long and narrow. Parietal callus smooth. Outer lip only slightly flaring, its inner surface smooth with the exception of a few faint, spirally elongated denticles on the adapical and abapical part. Sinus small. Base of columella bent backward.

Holotype: NMB H 17848 (Figure 21B-D).

Dimensions of holotype: Height 81.6 mm; width 51.4 mm.

Type locality: NMB locality 12887 (= PJ 1015). North slope of Cerro Barrigón, Araya Peninsula, Venezuela (Figure 21). Cerro Negro Member of Cubagua Formation (early Pliocene).

Remarks: This species is based on eight incomplete, partly fragmentary specimens. The holotype is the most complete shell.

Comparisons: S. barrigonensis cannot be compared directly with any of the species described herein. There is a superficial resemblance to S. fetus n. sp., but that species has a larger apical angle, a much more prominent spiral sculpture on the body whorl, and more knobs per whorl. The form recorded below under the name of Strombus (Lentigo) species A is much more slender and



Figure 26. A–D. Strombus (Lentigo) fetus Jung & Heitz, sp. nov. NMB H 17854. Holotype. NMB locality 18677: north coast of Escudo de Veraguas, Bocas del Toro, Panama; 1 km east of Long Bay Point. Escudo de Veraguas Formation (late Pliocene). Height 64.4 mm, width 48.8 mm. A. Front view. B. Rear view. C. From right side. D. From left side. E. Strombus (Lentigo) cf. fetus Jung & Heitz, sp. nov. NMB H 17855. NMB locality 18734: 300 m westnorthwest of Punta Piedra Roja, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (middle Pliocene). Height 46.1 mm, width 28.2 mm. Rear view. Both specimens ×1.5.

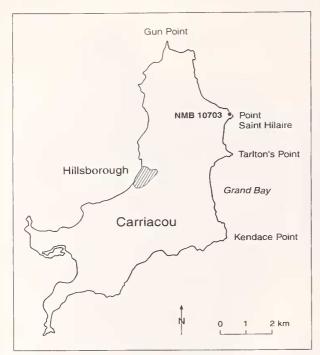


Figure 27. Map of the island of Carriacou, Grenadines, Lesser Antilles, showing NMB locality 10703, where *S.* cf. *insulanus* Jung & Heitz, sp. nov. has been found (for general location see number 12 of Figure 1).

lacks the fairly prominent axial threads on the body whorl. For comparative remarks concerning *S. toroensis* see under that species.

Material: There are only two lots with a total of eight specimens as listed below:

- 4 spec., NMB locality 12887 (= PJ 1015): north slope of Cerro Barrigón, Araya Peninsula, Venezuela. Cerro Negro Member of Cubagua Formation (early Pliocene). Holotype and 3 paratypes.
- 2. 4 spec., NMB locality 17532 (= GS-8-ARY): same locality as NMB locality 12887 (see above). Paratypes.

Measurements: Due to the incomplete preservation of the available specimens, no meaningful measurements can be made.

Occurrence: Known only from the type locality: North slope of Cerro Barrigón, Araya Peninsula, Venezuela. Cerro Negro Member of Cubagua Formation (early Pliocene).

Strombus (Lentigo) toroensis Jung & Heitz, sp. nov. (Figures 23, 24)

Etymology: Referring to the Province of Bocas del Toro.

Description: Shell reaching a height of about 70 mm,

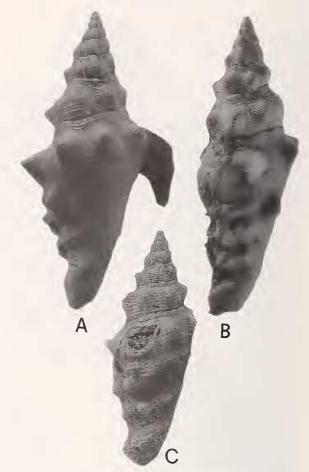


Figure 28. A. B. *Strombus (Lentigo) insulanus* Jung & Heitz, sp. nov. NMB H 17842. Holotype. NMB locality 18668: near the middle of the north coast of Escudo de Veraguas, Bocas del Toro, Panama. Escudo de Veraguas Formation (middle Pliocene). Height 53.2 mm, width 29.0 mm. A. Front view. B. From left side. C. *Strombus (Lentigo)* cf. *insulanus* Jung & Heitz, sp. nov. NMB H 17846. NMB locality 10703: 150 m northwest of Point Saint Hilaire, Carriacou, Grenadines, Lesser Antilles. Grand Bay Formation (early middle Miocene). Height 41.9 mm, width 16.6 mm. Rear view. Both specimens ×1.5.

moderately slender. Protoconch and earliest teleoconch whorls not known. Earliest preserved teleoconch whorls sculptured by three primary axial ribs per whorl with first five, then four, and later three and two secondary axial riblets in their interspaces. Primary and secondary axial ribs are all over-ridden by 10 spiral riblets. Secondary spiral riblets are introduced at an early stage. On later teleoconch whorls there are 10 subequal knobs per whorl, which become somewhat pointed on the body whorl. Number of knobs on body whorl nine. Dorsal surface of body whorl with three spiral rows of knobs. The most adapically situated row not prominent, the central row prominent, and the third, most abapically situated row less prominent than the central row. Remainder of dorsal



Figure 29. Strombus (Lentigo) sp. A. A, B. NMB locality 17530: 30 m west of Carrizal Cemetery, a little less than 3 km northeast of La Vela, Falcón, Venezuela. Mataruca Member of Caujarao Formation (late Miocene). A. NMB H 17850. Rear view. Height 59.0 mm, width 36.8 mm. B. NMB H 17851. From left side. Height 62.7 mm. Both specimens ×1.5.

surface of body whorl sculptured by numerous faint axial and spiral threads. Aperture long and narrow. Parietal callus smooth. Outer lip a little flaring, its inner surface smooth except for a few spirally enlongated denticles near the shallow sinus. Base of columella bent backward.

Holotype: NMB H 17865 (Figure 23A-D)

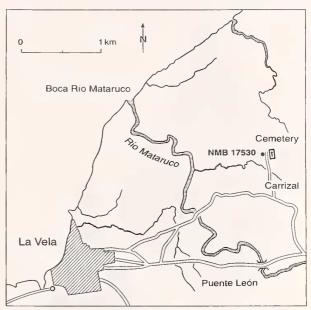


Figure 30. Map of the area northeast of La Vela, Falcón, Venezuela, showing NMB locality 17530, where *S.* sp. A is recorded from (for general location see number 9 of Figure 1).

Dimensions of holotype: Height 69.3 mm; width 42.3 mm.

Type locality: NMB locality 17635 (= PJ 1817 = CJ-87-32-01 = PPP 00201): northeast coast of Cayo Agua, Bocas del Toro, Panama; about 1.3 km southeast of Punta Norte (Figure 23). Cayo Agua Formation (early Pliocene).

Remarks: This species is based on two specimens from the same locality. The smaller specimen, the figured paratype (Figure 24E) is an incompletely preserved shell consisting of three late whorls and the adaptical part of the aperture. The holotype is more complete and consists of five and a half teleoconch whorls.

Comparisons: S. toroensis is somewhat similar to S. barrigonensis, but at the same time clearly distinct from it. S. barrigonensis is sculptured by eight subequal axial ribs on early teleoconch whorls, whereas S. toroensis has three primary axial ribs per whorl with secondary axial riblets in the interspaces. Both species have a similar apical angle. The base of the columella is more strongly bent backward in S. toroensis.

Material: As mentioned above, only two specimens from the same locality are available.

Measurements: Due to the incomplete preservation no meaningful measurement can be made.

Occurrence: Known only from the type locality: about 1.3 km southeast of Punta Norte, Cayo Agua, Bocas del

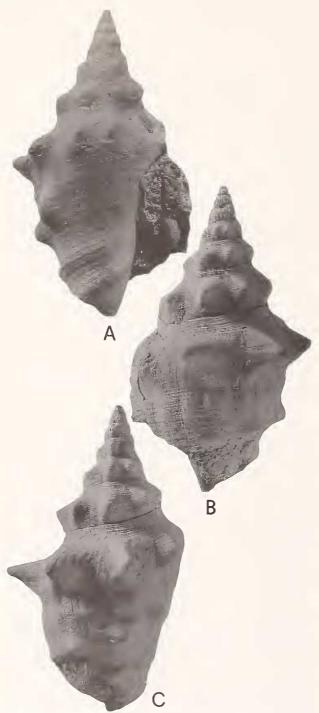


Figure 31. Strombus (Lentigo) sp. B. A–C. NMB H 17852. NMB locality 18716: southwest coast of Valiente Peninsula, Bocas del Toro, Panama; 5 km southeast of Cayo Patterson, at south end of Playa Lorenzo. Nancy Point Formation (late Miocene). Height 54.9 mm, width 34.1 mm. A. Front view. B. Rear view. C. From left side. ×1.5.

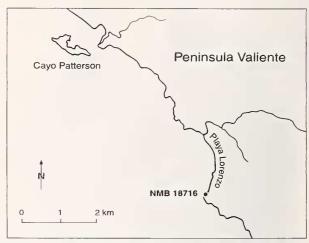


Figure 32. Map of part of the southwestern coast of the Valiente Peninsula, Bocas del Toro, Panama, showing NMB locality 18716, where *S.* sp. B has been found (for general location see number 5 of Figure 1).

Toro, Panama (Figure 23). Cayo Agua Formation (early Pliocene).

Strombus (Lentigo) fetus Jung & Heitz, sp. nov. (Figures 25, 26A–D)

Etymology: Latin fetus = full, filled, pregnant.

Description: Shell reaching a height of about 65 mm, rather stout. Protoconch not known. Earliest teleoconch whorls corroded. Number of preserved teleoconch whorls

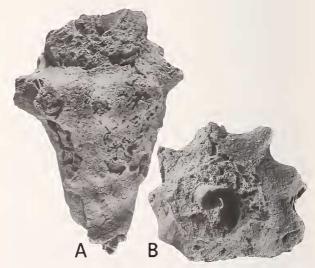


Figure 33. Strombus (Lentigo) sp. C. A, B. NMB H 17858. NMB locality 17526: 200 m south of El Porvenir and 7 km westnorthwest of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela. El Porvenir beds (middle or late Miocene). Height 44.2 mm, width 31.3 mm. A. Rear view. B. Apical view. ×1.5.

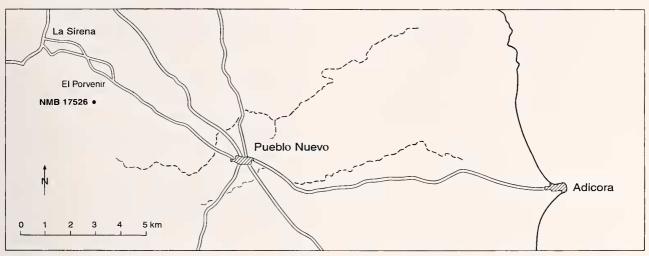


Figure 34. Map of part of the central Paraguaná Peninsula, Falcón, Venezuela, showing NMB locality 17526, where S. sp. C has been found (for general location see number 8 of Figure 1).

eight. Sculpture of early teleoconch whorls consists of 20 or a little more axial ribs, which are crossed by nine spiral threads. A shoulder situated a little below the middle of the height of the whorl is gradually developed. Simultaneously that part of the axial ribs situated above the developing shoulder gradually disappears. The axial ribs then are transformed into moderately prominent knobs. Profile of whorls above the shoulder straight on earlier whorls, somewhat concave on later whorls. Number of knobs on late whorls 12 to 13. Dorsal surface of body whorl sculptured by 10 primary spiral ribs below the shoulder and one to two secondary spiral threads on some of the interspaces. There are two spiral ridges with more prominent knobs below the shoulder. Growth lines near the outer lip prominent. Sculpture on and above the

shoulder consists of nine spiral riblets near the outer lip. Aperture long and narrow. Outer lip flaring. Parietal callus smooth except for a few spirally directed wrinkles near the adapical end of the aperture. Inner surface of outer lip smooth with the exception of a few spirally ori-

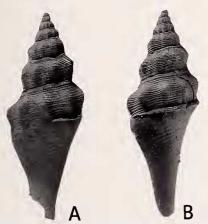


Figure 35. Strombus (Lentigo) sp. D. A, B. NMB H 17863. NMB locality 17439: 400 m south of Boca Quebrada Corotú, east coast of Burica Peninsula, Chiriquí, Panama. Armuelles Formation (Pleistocene). Height 36.9 mm, width 14.3 mm. A. Rear view. B. From left side. ×1.5.

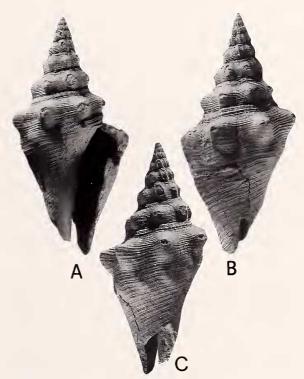


Figure 36. Strombus (Lentigo) sp. E. A-C. NMB H 17864. NMB locality 10635: Bowden, Port Morant, Jamaica. Bowder. Formation (early Pliocene). Height 42.3 mm, width 20.6 mm. A. Front view. B. Rear view. C. From left side. ×1.5.

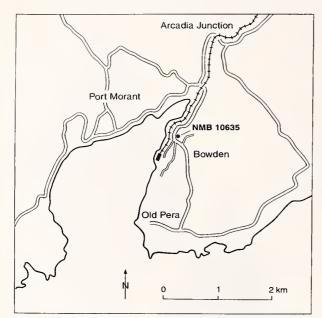


Figure 37. Map of the Port Morant area, southeastern Jamaica, showing NMB locality 10635, where *S.* sp. E has been found (for general location see number 17 of Figure 1).

ented wrinkles near the adapical end of the aperture. Stromboid sinus near the abapical end of the aperture rather shallow. Base of columella bent backward.

Holotype: NMB H 17854 (Figure 25A-D).

Dimensions of holotype: Height 64.4 mm; width 48.8 mm.

Type locality: NMB locality 18677 (= PJ 2214 = PPP 02178): north coast of Escudo de Veraguas, Bocas del Toro, Panama; 1 km east of Long Bay Point. Escudo de Veraguas Formation (late Pliocene). See Figure 25.

Remarks: The holotype and only specimen is fairly complete. The protoconch, the adapical part of the outer lip, and the extreme base are missing. In addition, a good portion of the dorsal surface is strongly corroded, thus leaving the spiral row of knobs on the dorsal part of the body whorl—the diagnostic feature of the subgenus *Lentigo*—not clearly recognizable.

Comparisons: With the exception of a fragment from Cayo Agua identified as S. cf. fetus, S. fetus is not related to any of the species reported herein. It is stouter and proportionately shorter than any of them, and its apical angle is larger. In this last respect it vaguely resembles S. lentiginosus, which, however, is characterized by three to four spiral rows of prominent knobs on the dorsal part of its body whorl, whereas S. fetus has two spiral ridges with occasional knoblike elevations.

S. fetus resembles S. raninus only superficially. Although the general shape and the apical angle are similar,

the two last knobs on the shoulder of the body whorl are not as developed as the spines in *S. raninus*.

Material: This species is based on a single specimen, the holotype.

Occurrence: Known only from the type locality (Figure 25).

Strombus (Lentigo) cf. fetus Jung & Heitz, sp. nov.

(Figures 23, 26E)

Remarks: A single fragment (NMB H 17855) from Cayo Agua, Panama, is available. It consists of the outer lip (base missing) and a portion of the dorsal side of the body whorl. The whole surface of the fragment is somewhat worn.

Comparisons: This fragment can only be compared to the corresponding part of the holotype of *S. fetus*. The sculpture of the two specimens is almost identical. *S. fetus* has a few more and finer spiral ridges on and above the shoulder. A feature developed in both specimens is a bulge near the outer lip extending parallel to it for some distance.

Occurrence: NMB locality 18734 (= PJ 2271 = PPP 02237). 300 m WNW of Punta Piedra Roja, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation, middle Pliocene (early Pliocene according to Dowsett & Cotton, 1996:71, fig. 3.12). See Figure 23.

Strombus (Lentigo) insulanus Jung & Heitz, sp. nov.

(Figures 25, 28A, B)

Etymology: Latin *insulanus* = inhabitant of an island.

Description: Shell reaching a height of about 55 mm, slender. Protoconch and earliest teleoconch whorls not known. Number of preserved teleoconch whorls eight. Sculpture of early teleoconch whorls consists of three varix like axial ribs and two smaller axial ribs in each interspace. These are crossed by six to eight spiral threads. On successive whorls secondary spiral threads appear. On later whorls the spiral threads become subequal in strength, and, at the same time, the axial ribs change their shape into subequal knobs situated on a gradually developing shoulder. There are nine moderately pointed knobs on the last whorl. Dorsal surface of body whorl not preserved, but left side of body whorl clearly shows three spiral rows of small knobs, which—as well as their interspaces—are sculptured by spiral threads. Outer lip not preserved with the exception of its adapical part. Parietal callus smooth. Inner surface of preserved part of outer lip smooth. Base of columella bent backward.

Holotype: NMB H 17842 (Figure 28A, B).

Dimensions of holotype: Height 53.2 mm; width 29.0 mm.

Type locality: NMB locality 18668 (= PJ 2205 = PPP 02169): near the middle of the north coast of Escudo de Veraguas, Bocas del Toro, Panama. Escudo de Veraguas Formation (middle Pliocene). See Figure 25.

Remarks: This species is based on a single specimen, the holotype. It is incompletely preserved: most of the outer lip and the dorsal part of the body whorl are missing, and the dorsal part of the penultimate whorl is damaged. As mentioned above, the protoconch and the earliest teleoconch whorls are not preserved. Despite these unsatisfactory circumstances, we decided that this species should be described formally.

Comparisons: S. insulanus is not closely related to any of the species discussed herein with the exception of the form called S. cf. insulanus hereafter from the early middle Miocene Grand Bay Formation of Carriacou, Grenadines, Lesser Antilles. Both have a similar sculpture on the early teleoconch whorls, and their apical angle is similar as well. S. cf. insulanus is smaller than S. insulanus and shows only two (instead of three) spiral rows of knobs on the left side of the body whorl.

Occurrence: Known only from the type locality (see above).

Strombus (Lentigo) cf. insulanus Jung & Heitz, sp. nov.

(Figures 27, 28C)

Remarks: This species is represented by a single, incomplete specimen (NMB H 17846) from the Grand Bay Formation of Carriacou, Lesser Antilles. Its outer lip and the dorsal part of its body whorl are not preserved, the ventral portion of its penultimate whorl is damaged, and its protoconch and earliest teleoconch whorls are missing.

Similarities and differences between this species, which was listed as *Strombus* sp. by Jung (1971, table 2), and *S. insulanus* are mentioned under the latter.

Occurrence: NMB locality 10703 (= PJ 785): 150 m NW of Point Saint Hilaire, Carriacou, Grenadines, Lesser Antilles. Grand Bay Formation (early middle Miocene) (Robinson & Jung, 1972: 114, 125). See Figure 27.

Further Occurrences of the Subgenus Lentigo

So far we have dealt with material that is sufficiently well preserved to be named or to allow the use of open nomenclature. However, there is additional, though scarce, material that cannot possibly be identified specifically. The scarcity of material dictates ignorance of variability. However, it is well known that species of *Strom*-

bus vary considerably. That this applies to species of the subgenus *Lentigo* as well is beautifully documented by the living Eastern Pacific *Strombus (Lentigo) granulatus* Swainson. We have referred to this variability in the discussion of that species.

For reasons of simplicity, the species recorded hereafter are identified by the letters A to E. The majority of these five species are represented by a single specimen.

Strombus (Lentigo) sp. A

(Figures 29, 30)

Remarks: Twelve incomplete specimens from the late Miocene of Falcón, Venezuela are available. They are all not well preserved. One of the figured specimens (Figure 29B) clearly shows two spiral rows of knobs on the dorsal side of the body whorl, the most diagnostic feature of the subgenus *Lentigo*.

Occurrence: NMB locality 17530 (= GS-1-FLCN): 30 m west of the Carrizal Cemetery, a little less than 3 km northeast of La Vela de Coro, Falcón, Venezuela (see Figure 30). Mataruca Member of Caujarao Formation (late Miocene); *Globorotalia acostaensis* zone (Díaz de Gamero, 1977:83; see also Jung, 1989:20).

Strombus (Lentigo) sp. B

(Figures 31, 32)

Remarks: Three specimens from the Pliocene of the Valiente Peninsula, Bocas del Toro, Panama are available. Two of them represent spires of juvenile individuals, the third one seems to be an adult shell, the base of which, however, is not preserved.

The protoconch and the earliest teleoconch whorls are not preserved. The earliest preserved sculpture consists of three axial swellings per whorl and four axial ribs in each interspace. These are crossed by 10 spiral threads. On succeeding whorls the axial sculptural elements become subequal in size until they eventually develop into axially elongated knobs of the same size.

On the shoulder of the apparently adult specimen mentioned above there are nine knobs, the last four of which are pointed. The preserved part of the dorsal side of its body whorl carries two spiral rows of knobs.

Occurrence: NMB locality 18716 (= PJ 2253 = PPP 02217): southwest coast of Valiente Peninsula, Bocas del Toro, Panama, 5 km southeast of Cayo Patterson, at south end of Playa Lorenzo (see Figure 32). Very top of Shark Hole Point Formation (Pliocene).

Strombus (Lentigo) sp. C

(Figures 33, 34)

Remarks: A single poorly preserved specimen (NMB H 17858) from the middle or late Miocene of the Paraguaná

Peninsula, Venezuela, is available. The body whorl without the outer lip and a small part of the penultimate whorl are preserved. The shoulder carries nine to 10 knobs, the last five of which are pointed. On the dorsal side of the body whorl there are two spiral rows of knobs.

Occurrence: NMB locality 17526 (= GS-94-PGNA): 200 m south of El Porvenir and 7 km WNW of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela (see Figure 34). El Porvenir beds (middle or late Miocene, not early Miocene as indicated by Gibson-Smith & Gibson-Smith, 1979:14).

Strombus (Lentigo) sp. D

(Figures 10, 35)

Remarks: A single immature specimen (NMB H 17863) from the Pleistocene of the Burica Peninsula, Panama is available. It consists of seven whorls. The protoconch and the earliest teleoconch whorls are not preserved. It has been collected from the same locality as a specimen of *S. granulatus* (Figures 6E–G, 10) but represents a different species. *S.* sp. D seems to have more teleoconch whorls than *S. granulatus*; it has only eight spiral threads on the early teleoconch whorls as opposed to 11 to 13 in *S. granulatus*. On the last whorl of *S.* sp. D only a weakly developed spiral row of knobs can be recognized which is situated a little distance below the shoulder.

Occurrence: NMB locality 17439 (= PJ 1757): 400 m south of Boca Quebrada Corotú, east coast of Burica Peninsula, Chiriquí, Panama (see Figure 10). Armuelles Formation (Pleistocene).

Strombus (Lentigo?) sp. E

(Figures 36, 37)

Remarks: A single somewhat immature specimen (NMB H 17864) from the early Pliocene of Jamaica is available. It consists of almost eight teleoconch whorls and a small part of the protoconch. The sculpture of the early teleoconch whorls consists of three axial swellings per whorl and two to three axial ribs in each interspace. All these axial sculptural elements are crossed by eight primary spiral threads on early teleoconch whorls. On succeeding whorls, secondary spiral threads are introduced, and at the same time, the axial swellings and ribs gradually become equal in size. The shoulder of the last preserved whorl carries seven slightly pointed knobs. The edge of the outer lip is not preserved. Its smooth inner surface carries a number of narrow lirae. The base is broken. On the last whorl there is a spiral row of knobs situated a little distance below the shoulder. Additional, more complete material from Bowden is needed to show whether a second row of knobs is developed on the body whorl. For this reason the single available specimen is only tentatively assigned to the subgenus Lentigo.

Occurrence: NMB locality 10635: Bowden, Port Morant, Jamaica (see Figure 37). Bowden Formation (early Pliocene).

Acknowledgments. We thank Dr. James McLean, LACM (Los Angeles, California) for the loan of specimens under his care, and Marcos Alvarez, Panama City, for the loan of specimens from his private collection. We are indebted to Alison Trew, National Museum of Wales, Cardiff, Great Britain, for information concerning an old type specimen; to Kathie Way, BMNH, for providing literature not available in Basel; and to Dr. Gary Rosenberg, ANSP, for pointing out and providing copies of relevant literature from his World Wide Web database of living marine West Atlantic gastropods.

We furthermore thank Dr. Jon Todd, formerly a postdoc at the NMB, now at BMNH, for constructive discussions and additional material; Dr. Richard Guggenheim and Daniel Mathys, both of the Scanning Electron Microscope Laboratory of the University of Basel, Switzerland, and Severino Dahint, photographer at the Naturhistorisches Museum Basel, for the photographic illustrations; and Dr. Anthony Coates, Smithsonian Tropical Research Institute, Panama, for information concerning the absolute ages given in Table 1.

Last, but not least, we are grateful to the Kugler Foundation, Basel, for covering the costs of field work, and to the Smithsonian Tropical Research Institute, Panama, for the facilities offered during field work.

LITERATURE CITED

Abbott, R. T. 1960. The genus *Strombus* in the Indo-pacific. Indo-Pacific Mollusca 1(2):33–146.

ABBOTT, R. T. 1974. Pp. 1–663 in American Seashells. 2nd ed. Van Nostrand Reinhold Company: New York, Cincinnati, Toronto, London, Melbourne.

Bales, B. R. 1942. A new subspecies of *Strombus raninus* Gmelin. The Nautilus 56(1):18–19.

CLENCH, W. J. & R. T. ABBOTT. 1941. The Genus *Strombus* in the Western Atlantic. Johnsonia 1(1):1–16.

Dall, W. H. 1890. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Transactions of the Wagner Free Institute of Science of Philadelphia 3(I):1–200.

Díaz DE Gamero, M. L. 1977. Revisión de las edades de las unidades litoestratigráficas en Falcón central en base a su contenido de foraminíferos planctónicos. Memorias quinto Congreso geologico venezolano 1:81–86.

Dowsett, H. J. & M. A. Cotton. 1996. Graphic correlation of marine deposits from the Central American Isthmus: implications for late Neogene paleoceanography Pp. 57–75 in J.B.C. Jackson, A.F. Budd & A.G. Coates (eds.), Evolution and Environment in Tropical America. The University of Chicago Press.

DURHAM, J. W. 1950. 1940 E. W. Scripps cruise to the Gulf of California. Part II: Megascopic paleontology and marine stratigraphy. Geological Society of America, Memoir 43:1– 216.

DURHAM, J. W. 1962. New name for *Strombus granulatus* subsp. *acutus* Durham, 1950, not Perry, 1811. The Veliger 4(4): 213.

EMERSON, W. K. & W. E. OLD. 1963. Results of the Puritan-American Museum of Natural History Expedition to Western Mexico. 19. The recent mollusks: Gastropoda, Strom-

- bacea, Tonnacea, and Cymatiacea. American Museum Novitates 2153:1-38.
- GIBSON-SMITH J. & W. GIBSON-SMITH. 1979. The genus *Arcinella* (Mollusca: Bivalvia) in Venezuela and some associated faunas. Geos 24:11–32.
- GMELIN, J. F. 1791. Caroli a Linné Systema naturae per regna tria naturae. Editio decima tertia. v. 1, pt. 6, cl. 6, Vermes: 3021–3910.
- GRANT, U. S. & H. R. GALE. 1931. Catalogue of the Marine Pliocene and Pleistocene Mollusca of California and Adjacent Regions. San Diego Society of Natural History, Memoir 1, 1036 pp.
- Humfrey, M. 1975. Sea Shells of the West Indies. Taplinger Publishing Company: New York. 351 pp.
- IREDALE, T. 1921. Molluscan nomenclatural problems and solutions. Proceedings of the Malacological Society of London 14:198-208
- Jousseaume, F. P. 1886. Coquilles marines des côtes d'Abyssinie et de Zanzibar recueillies par M. Raffray en 1873 et en 1874. Le Naturaliste 8(28):220–222.
- JUNG, P. 1971. Fossil mollusks from Carriacou, West Indies. Bulletins of American Paleontology 61(269):143–262.
- JUNG, P. 1989. Revision of the *Strombina*-Group (Gastropoda: Columbellidae), Fossil and Living. Distribution, Biostratigraphy, Systematics. Schweizerische paläontologische Abhandlungen 111. 298 pp.
- KEEN, A. M. 1971. Sea Shells of Tropical West America. 2nd ed. Stanford University Press: Stanford, California. XIV + 1064 pp.
- LAMARCK, J. 1822. Histoire naturelle des animaux sans vertèbres 7. Paris. 711 pp.
- LINNAEUS, C. 1758. Systema naturae per regna tria naturae. Editio decima, reformata, 1. Stockholm. 824 pp.
- LIPKA, D. A. 1974. Mollusks. Pp. 141–196 In T. J. Bright & L. H. Pequegnat (eds.), Biota of the West Flower Garden Bank Gulf Publishing: Houston, Texas.
- LOZOUET, P. & P. MAESTRATI. 1986. Le *Strombus granulatus* Swainson, 1822, une relique mésogéenne. Xenophora (Bulletin de l'Association Française de Conchyliologie) 31:11–15.
- MACSOTAY, O. & W. S. MOORE. 1974. Cronoestratigrafía de algunas terrazas cuaternarias marinas del nororiente de Venezuela. Cuadernos azules 12. Caracas. 65 pp.

- Mawe, J. 1823. The Linnaen System of Conchology, Describing the Orders, Genera, and Species of Shells, Arranged into Divisions and Families. London. i–xv + 207 pp.
- MONTFORT, DENYS DE. 1810. Conchyliologie systématique et classification méthodique de coquilles 2. Paris. 676 pp.
- ODÉ, H. 1982. Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph), Part II: Gastropoda. Texas Conchologist 19:10–21.
- Perry, G. 1811. Conchology, or the Natural History of Shells. London. 4 pp.
- Petuch, E. J. 1994. Atlas of Florida Fossil Shells (Pliocene and Pleistocene Marine Gastropods). Chicago Spectrum Press: Evanston, Illinois. XII + 394 pp., 20 figs., 100 pls.
- RICE W. H. & L. S. KORNICKER. 1962. Mollusks of Alacran Reef, Campeche Bank, Mexico. Publications of the Institute of Marine Science 8:366–403.
- Rios, E. C. 1985. Seashells of Brazil. Río Grande, RS, Empresas Ipiranga. 328 pp.
- ROBINSON, E. & P. Jung. 1972. Stratigraphy and age of marine rocks, Carriacou, West Indies. Bulletin of the American Association of Petroleum Geologists 56(1):114–127.
- SAUNDERS, J. B., P. JUNG & B. BIJU-DUVAL. 1986. Neogene Paleontology in the Northern Dominican Republic. 1. Field surveys, lithology, environment, and age. Bulletins of American Paleontology 89(323). 79 pp.
- SHOEMAKER, A. H. 1971. Strombus range extensions. The Nautilus 85:72.
- Springer, S. & H. R. Bullis. 1956. Collections by the "Oregon" in the Gulf of Mexico. Special Scientific Report: Fisheries 196, ii+134 pp.
- SWAINSON, W. 1822. A Catalogue of the Rare and Valuable Shells, Which Formed the Celebrated Collection of the Late Mrs. Bligh. With an Appendix, Containing Scientific Descriptions of Many New Species, and Two Plates. London. 60 pp.
- VOKES, E. H. 1989. Neogene Paleontology in the northern Dominican Republic. 8. The Family Muricidae (Mollusca: Gastropoda). Bulletins of American Paleontology 92(332):1–94.
- WHITTAKER, J. E. 1988. Benthic Cenozoic Foraminifera from Ecuador: Taxonomy and Distribution of Smaller Benthic Foraminifera from Coastal Ecuador (Late Oligocene–Late Pliocene). British Museum (Natural History): London. xi, 194 pp.